AVIAN DISPERSAL AND DEMOGRAPHY: SCALING UP TO THE LANDSCAPE AND BEYOND

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The astonishing diversity of avian movement patterns, reproductive tactics, and survival rates creates rich opportunities for study, but also presents enormous challenges for explaining variation among life-history traits and dispersal. Dispersal decisions shape the genetic structure of populations and thus can be of considerable importance in processes such as speciation. Moreover, a better understanding of dispersal and movement among populations remains fundamental for effective conservation strategies for a great many species. Factors affecting dynamics of highly mobile bird populations are particularly difficult to decipher because of varying environmental conditions and habitat changes among breeding, migration, and wintering areas. Depending on species, dispersal by individual birds involves movements of <0.1 to >1000 km (Greenwood and Harvey 1982). Therefore, hypotheses about survival, reproductive rates, population dynamics, and conservation actions must be addressed at much larger spatial scales than has typically been considered in the past, and in some instances should span entire continents or hemispheres.

Fortunately, there has been recent progress in both the conceptual development and application of techniques that have led to a better understanding of linkages between breeding and wintering grounds (Hobson 1999, Webster et al. 2002), and analytical methods for estimating movement, occupancy, and survival rates (Nichols and Kaiser 1999, Kendall and Nichols 2004). Furthermore, we anticipate exciting advances in the near future, as information about natal, breeding, or wintering locations of birds is integrated with information on subsequent dispersal decisions and demographic performance. These premonitions sparked our interest in hosting a special session on this topic at the 121st annual meeting of the AOU in Urbana-Champaign, Illinois, August 2003. We also sought to expand on ideas and studies presented by Walters (2000), by focusing on both new empirical evidence and ways of revealing dispersal patterns and processes at large spatial scales.

The ranges of distances reportedly dispersed by young birds between fledging and first nesting (i.e., natal dispersal; Greenwood and Harvey 1982) and by adult birds between breeding attempts (i.e., breeding dispersal) are obviously constrained by study-area size (Lambrechts et al. 1999) and detection methods (Koenig et al. 1996). Choice of correct scale for evaluating causes and consequences of natal dispersal would seem particularly important (Forero et al. 2002) in view of (1) longer distances typically moved by young or inexperienced birds and (2) potentially high mortality associated with postfledging movements, which could be counteracted by benefits of site familiarity. In a novel investigation of breeding dispersal by Tree Swallows (*Tachycineta bicolor*), Winkler et al. (2004) demonstrate that adults disperse less far than the detection limits of their large scale monitoring scheme in upstate New York, a system in which birds could be detected moving among widely spaced study units located up to 400 km apart. However, they also report frequent breeding dispersal by females with reproductive failure to sites beyond the boundaries of study units typical of most passerine study-area sizes.

Methods of estimating movement rates have been developing rapidly, with new models being developed

and with widely available estimation software becoming increasingly user-friendly. Kendall and Nichols (2004) provide a succinct summary of direct and indirect methods for estimating survival and occupancy rates, estimates that can be obtained by even the most computer illiterate among us who is willing to consult a helpful statistician! Arguably, the most notable enhancements have occurred by merging different types of re-encounter information (e.g., by combining band recovery with radio-telemetry or mark-resighting data), advances that continue to appear at a rapid pace (e.g., Blums et al. 2002; references in Kendall and Nichols 2004). Indeed, Powell's (2004) extension of multistate modeling to conduct *a posteriori* enhancements of recapture data using ancillary information (e.g., isotopic, genetic or other reliable tracer) sets the stage for rapid methodological development and applications in avian ecology and conservation. We are unaware of existing field data to apply to Powell's (2004) multistate modeling method but suggest, for instance, that isotopic study of sequential feather samples from the same marked individuals would be most informative. In some cases model extensions will be needed, for example to incorporate classification uncertainty associated with isotopic identification of prior location, but the power of such *a posteriori* enhancements is such that model extensions are likely to be forthcoming.

We also believe that there are exciting opportunities for combining molecular-genetic data with capture-recapture data on marked animals. Kendall and Nichols (2004) briefly discuss two classes of methods by which genetic data can be used to draw inferences about movement. One class involves inferences about the genetic similarity of each captured individual with other individuals in the sampled population, and thus about the likelihood that the individual was a product of reproduction in the population or an immigrant from elsewhere (Waser and Strobek 1998, Hansson et al. 2003). We can envision several ways to make joint use of such data and capture-recapture data, including an analog of the approach used by Powell (2004). The other class of methods permitting inference from genetic data involves use of gene-frequency data from multiple subpopulations in conjunction with classic genetic models of subdivided populations (Wright 1943). Differences in gene frequencies among subpopulations are used to inform model dispersal parameters (Rousset 2001), and we anticipate development of joint likelihoods that include these models as well as capture-recapture models using data on marked individuals. The movement parameters of the capture-recapture models should be proportional to the dispersal parameters of the gene-frequency models, permitting simultaneous inference using these disparate data sources.

Explicit linkages between wintering and breeding habitats or locations of migratory songbirds made with stable-isotope techniques (Marra et al. 1998, Rubenstein et al. 2002, Bearhop et al. 2004) are now being extended to determine potential sources of immigrant birds, an exciting development that could help to pinpoint source populations, exchange among populations, and origins of birds following large-scale shifts in species' distributions (Hobson 2002). Hobson et al. (2004) apply stable-isotope analyses to determine the frequency of long-distance dispersal by adult and first-year migrant songbirds, a group of birds for which traditional banding or radio-tracking techniques would yield limited information or be very difficult or unwise to use. Knowledge of likely origin could also shed light on the likelihood that a bird is a transient versus resident in formal mark-recapture analyses, and ultimately provide more rigorous tests of putative benefits of site fidelity in birds (Bensch et al. 1998). Isotopic and mark-recapture data have been combined to provide new insights into effects of winter weather conditions on apparent annual survival of migratory songbirds (Mazerolle et al., in press). In this issue, by combining isotope and conventional banding techniques, Dugger et al. (2004) show that rainfall events on breeding and wintering areas affect survival and abundance of winter resident songbirds in different ways, perhaps via changes in survival during migration or breeding, or by altering interspecific interactions on wintering areas.

We are encouraged by rapid advances in theory and application of these and other approaches for dispersal studies. However, we also recognize that these methodological advances require close scrutiny. For example, confidence in inferences based on isotopic analyses will require new laboratory and field studies to fully characterize natural isotopic gradients and to determine sources of variation in tissue isotope signals, timing and patterns of molt, and tissue-turnover or claw-growth rates (Rubenstein and Hobson 2004). Likewise, integration of different data sources pertaining to movements and survival rates needs refinement and field testing, not just with simulation but also with actual field tests where true survival, reproductive, and movement rates are known. With careful study design and innovation, the next decade should produce remarkable improvement in our understanding of the demographic implications of varying dispersal and migration patterns.

ACKNOWLEDGMENTS

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